

Classification of the Subtribe Carabina (Coleoptera, Carabidae) Based on Molecular Phylogeny

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Abstract A new higher classification of the subtribe Carabina constructed from the molecular genealogical tree is proposed. This is the first attempt to employ the result of molecular phyloanalysis into the taxonomy of the Carabina on the world-wide basis. In the new system, the Carabina is classified into 29 divisions and 137 genera.

According to the recent technological progress of the molecular biology, it has become possible to throw an objective light on the evolutionary history and the phylogenetic relationships of many kinds of organisms by analyzing the gene sequences of DNA, and this trend has been extended to the field of entomology for the past several years. A molecular phylogenetical study of the subfamily Carabinae was expected by Syozo OSAWA, and has been expanded on a world-wide scale in collaboration with Zhi-Hui SU, Yûki IMURA and many other colleagues (*e.g.*, SU, OKADA *et al.*, 1996; IMURA, KIM *et al.*, 1998; IMURA, SU *et al.*, 1998; IMURA, ZHOU *et al.*, 1998; OSAWA *et al.*, 1999; SU, IMURA & OSAWA, 2001; OSAWA, SU & IMURA, 2002). As to the subtribe Carabina of the tribe Carabini, to which a special attention has been paid, all the samples submitted through the course of this study have been estimated at about 2,000 from nearly 500 sites of 35 countries, containing over 90% of supraspecific categories and more than 40% of the hitherto known species of the same subtribe. This seems to be sufficient to revise the phylogeny and the evolutionary history of the Carabina, and also to be worth applying the result into the taxonomy and the classification.

Since the first comprehensive work made by REITTER (1896), much has been attempted at the higher classification of the subtribe Carabina (so-called *Carabus* in a broad sense). Fundamentally, all the previous systems have been constructed based upon morphological features, and they fall roughly into three phases according to the employed characters, that is, external structure of the imago (*e.g.*, REITTER, 1896; LAPOUGE, 1929–'53; BREUNING, 1932–'37), that of the larva (*e.g.*, LAPOUGE, 1929; TURIN *et al.*, 1993 in part, DEUVE, '97 in part), and endophallic structure of the male genital organ (*e.g.*, ISHIKAWA, 1973, '78, '79; DEUVE, 1991, '94, '97; IMURA, 1996; IMURA & MIZUSAWA, 1996; BREZINA, 1999). Since the key characters adopted for evaluation were different according to the authors, any of them were inevitably affected by each author's subjective point of view. As a result, we have not yet reached the stan-

dard system widely approved by most taxonomists. In order to attain the persuasive system reflecting natural phylogeny, classification of the Carabina must be revised by more explicit procedure such as the molecular phyloanalysis.

In the present study, a new system is proposed for the higher classification of the subtribe Carabina down to the specific level by taking the result of molecular phyloanalysis into account. The genealogical trees on which the present study is mainly founded are those constructed by the neighbor-joining (NJ) method or unweighted pair-group method with arithmetic mean (UPGMA), analyzing 1,069 base-pairs of the mitochondrial gene encoding NADH dehydrogenase subunit 5 (ND5). It is the first attempt to reconstruct the supraspecific categories of a certain group of the Coleoptera on the world-wide basis by employing the findings of molecular genealogy. An earlier version of this paper was read at the symposium on the molecular phylogeny and evolution of the insects (11 February 2000), organized by the Biohistory Research Hall, Takatsuki, and was already sketched in Chapter 6 of the special issue recently published (OSAWA, SU & IMURA, 2002, pp. 125–135).

Status of the Subtribe Carabina

Taxonomic status of the subtribe Carabina in the present sense is basically equivalent to that traditionally defined by the morphology. All the molecular genealogical trees drawn by several methods indicate that the tribe Carabini is clearly divided into two distinct clusters, corresponding respectively to the subtribe Calosomina and Carabina (OSAWA *et al.*, 1999, p. 66; SU & KIM, 1999, p. 9; OSAWA, SU & IMURA, 2002, p. 52, fig. 4-8, p. 53, fig. 4-9, etc.). So far as the analyzed taxa are concerned, all the species morphologically defined as belonging to the Calosomina are by no means intermingled with those belonging to the Carabina on the tree, so that the possible phylogenetic relationships between the two subtribes suggested by ISHIKAWA (1978, pp. 66–68) is rejected.

In the new system, I avoid to regard the subtribe Carabina as equivalent to the genus *Carabus* LINNÉ as has been adopted by most taxonomists, but classify it into a number of distinct divisions and genera mainly for the following reasons:

1) As has been indicated by the molecular genealogical trees (SU, OKADA *et al.*, 1996, p. 176, fig. 1-a; IMURA, KIM *et al.*, 1998, p. 21, fig. 1; IMURA, SU *et al.*, 1998, p. 227, fig. 1; OSAWA *et al.*, 1999, p. 90, fig. 12; OSAWA, 1999, p. 16, fig. 1; SU, IMURA & OSAWA, 2001, p. 519, fig. 2; OSAWA, SU & IMURA, 2002, p. 49, fig. 4-5, p. 68, fig. 5-8, p. 202, fig. 9-1), the first diversification of the Carabina has taken place as an explosive radiation of the major groups. This means that the Carabina should be regarded as an assemblage of distinct lineages rather than simply be unified into a homogeneous group.

2) All the classifications should be minimally redundant and maximally informative. Regarding the subtribe Carabina as the equivalent of the genus *Carabus* (s. lat.), or in other words, injecting a single genus between subtribe and species con-

tributes no new information, since the diagnosis of the genus is the same as that of the subtribe (i.e., Carabina=*Carabus*). Note that, in this case, the classification does have one redundant name and it gives no more information on the detailed systematic position of each species under the binominal nomenclatural system. For example, “*Carabus blaptoides*” only informs us the message that this highly specialized carabid is a member of the genus *Carabus*. If we want to express its systematic position more precisely, we must add the subgeneric name in parentheses after *Carabus*. Inexpediently, these subgeneric names are often with very long spelling such as *Sphodristocarabus*, *Pseudocoptolabrus*, and so on. This is apparently inconvenient and less practical, above all in case we use many scientific names in a single paper.

Conventions for the Classification

To construct a new higher classification of the Carabina from the molecular genealogical tree, the Linnean Hierarchy is used, with certain conventions described as follows.

As has been mentioned in the preceding section, the subtribe Carabina is considered to have been split into nearly thirty clusters or branches emerged within a short period at the beginning of its radiation, and I regard each of them as corresponding to the division. The division in the present sense is a taxonomic rank settled below subtribe and above genus. Although not regulated by the International Code of Zoological Nomenclature (ICZN), I adopt this rank for the sake of convenience. In the present system, the Carabina is classified at first into twenty-nine divisions, and each division is further divided into two to five subdivisions where it is necessary. On the molecular genealogical tree, the branching order of these divisions cannot be determined with certainty because of low bootstrap values supporting the respective branches. This in turn neither implies a true multifurcation nor a failure to resolve a dichotomous situation. Rather, it unambiguously says that the order of the divisions in the list is interchangeable. I therefore regard all the divisions as *sedis mutabilis* (*sensu* WILEY, 1979).

The terminology of the supraspecific categories of the Carabina except for those properly described as genus or subgenus is confused. Not a few higher names with the rank of “division”, “subdivision”, “section” or “group” have been proposed by previous authors as summarized in Table 1. According to ICZN, these higher names are either not regulated (in case they are settled above generic rank, e.g., those proposed by LAPOUGE or ISHIKAWA) or deemed to be subgeneric names (in case they are proposed for a genus-group division of a genus, e.g., those by other authors; see Article 10.4). For example, a uninominal name Multistriati was first proposed by REITTER (1896) as one of the higher ranks settled between genus and subgenus, representing the eleven subgenera such as *Piocarabus*, *Euporocarabus*, *Oreocarabus*, and so on. Subsequently, the same term has been applied in different sense to various combinations of higher taxa by later authors (cf. LAPOUGE, 1929–’53; BREUNING, 1932–’37; ISHIKAWA, 1978; DEUVE, 1991; IMURA, 1996, etc.). In reality, however, Multistriati is deemed to be a

Table 1. Higher names of the subtribe Carabina either not regulated by ICZN or to be synonymized.

Author	Higher name
REITTER (1896)	Carabi angustoccephali, C. procerogenici, C. procrustogenici, C. macrocephali, C. cechenogenici, C. multisetosi, C. tribacogenici, C. glabriventri, C. latipalpi, C. crenolimbi, C. emarginati, C. morphogenici, C. multistriati, C. costiferi, C. glabripenni
BENGTTSSON (1927)	Archaeocarabus*, Metacarabus*, Neocarabus*
LAPOUGE (1929)	Carabes Rostrilabres* (Fissirostres, Obtusirostres, Conirostres, Ténuirostres, Lamellirostres), C. Quadricuspides* (Macrocerques, Brachycerques), C. Serrilabres* (Holodontes, Synodontes, Tétrodontes, Pentodontes); Psilogoniens, Pliochètes, Tribacogéniens, Multistriés, Carabogéniens
BREUNING (1932)	Carabi Brevimandibulares, C. Carabogenici, C. Multistriati, C. Longimandibulares
ISHIKAWA (1978)	Carabogenici, Spinulati, Multistriati
DEUVE (1991)	Spinulati, Digitulati, Lipastromorphi, Archicarabomorphi, Multistriati
DEUVE (1994)	Spinulati, Digitulati, Lipastromorphi, Archicarabomorphi, Lobifera
IMURA (1996)	Carabogenici (Digitulati, Lipastromorphi, Archicarabomorphi), Multistriati (Spinulati, Crenolimbi, Latitarsi, Arciferi, Procrustimorphi)
DEUVE (1997)	Spinulati, Digitulati, Lipastromorphi, Archicarabomorphi, Lobifera (Crenolimbi, Multistriati, M. Tomocaraboides, M. Oreocaraboides, Longimandibulares, Neocarabi)

Terms proposed by LAPOUGE and ISHIKAWA were settled between the subtribe Carabina and its component genera, and those proposed by other authors were settled between the genus *Carabus* (s. lat.) and its component subgenera. Terms denoted by asterisks indicate that they were proposed on the basis of the larval morphology.

subgenus of the genus *Carabus* (s. lat.) under Article 10.4 of ICZN, and is destined to be a synonym of a certain subgenus described previously, even if it becomes available by satisfying the provisions of Article 10. The same situations are also referable in the terms proposed by BENGTTSSON (1927), BREUNING (1932), DEUVE (1991, '94 and '97) and IMURA (1996). Those proposed by LAPOUGE (1929) and ISHIKAWA (1978) are not regulated by ICZN, yet their adoption and rejection are, if any, complicated (see again Table 1).

To avoid further confusion, I revoke these non-regulated names and propose to give new divisional names indicated by a compound word with the stem from that of the type genus and the suffix spelled *-genici*^{*)}. For example, the division composed of the three genera, *Heterocarabus* MORAWITZ, 1886, *Chaetocarabus* THOMSON, 1875, and *Platycarabus* MORAWITZ, 1886, is named “Chaetocarabigenici”. The benefit of this principle is that we can cope with the alternation of the component genera when it is necessary.

Each division as defined above is either constituted by a single taxon or further divided into two or more clusters or branches. In the former case, the division is deemed

^{*)} One of the oldest suffixes appended to the (sub)divisional names of the Carabina proposed by REITTER (1896).

to be composed of a single monotypical genus. In the latter situation, I regard each cluster or branch as corresponding to a distinct genus if the bootstrap confidence level at the branching point is constantly high (usually more than 70%). Each genus is further divided into two or more subgenera where it is necessary. If the morphological gaps in two or more taxa are large enough, they are distinguished, though conventionally, at the generic level, even though they belong to a single cluster on the tree (e.g., *Eupachys* and *Acoptolabrus*). In contrast, if two or more taxa fall respectively into different lineages on the tree, they are also discriminated at the generic level even if considered congeneric morphologically (e.g., *Leptocarabus* and *Sinoleptocarabus*).

In the present classification, I treat the taxa down to the specific level and a subject on the infraspecific categories is left untouched. In selecting specific names on the list, I basically follow the newest catalogue written by BŘEZINA (1999), which in turn means that those described after the latter half of 1999 are excluded except for several important species. As to the species whose DNAs have not yet been analyzed (shown in brackets), their positions are synthetically assumed in due consideration of morphology, zoogeography, ecology, and so on, above all of endophallic character and the distributional range. The type species of each (sub)genus is shown by the boldfaced letter.

In comparison with current classifications proposed after that by ISHIKAWA (e.g., DEUVE, 1991, '94, '97; IMURA, 1996; BŘEZINA, 1999), the main changes made in the present system are as follows:

1) The *Limnocarabus*–*Euleptocarabus* lineage (*Limnocarabigenici* in the present sense=*Lepidospinulati sensu* IMURA, KIM *et al.*, 1998) is separated at the divisional level from the *Apotomopterus* series (*Apotomopterigenici* in the present sense) (see IMURA, KIM *et al.*, 1998; OSAWA, SU & IMURA, 2002, pp. 69–72).

2) The division *Latitarsi* (*sensu* IMURA, 1996) (=Multistriati *Tomocaraboides* plus *M. Oreocaraboides* in the division *Lobifera*, *sensu* DEUVE, 1997) is not unified into a single category but is distinguished into seventeen different divisions not necessarily showing a close affinity with one another.

3) *Hygrocarabus*, which has been placed in various positions (*Chaetocarabus*, *sensu* ISHIKAWA, 1984; Multistriati, *sensu* DEUVE, 1991; *Lobifera*, *idem.*, 1994; Longimandibulares in *Lobifera*, *idem.*, 1997; Arciferi, *sensu* IMURA, 1996, etc.), is assigned to an independent division remote from the *Chaetocarabus* series.

4) *Ctenocarabus*+*Rhabdotocarabus* and *Cathoplius*, all having been placed in the so-called *Lobifera* lineage (*sensu* DEUVE, 1994, '97) or in the *Procrustimorphi* (*sensu* IMURA, 1996), are regarded as forming a distinct division, respectively.

In addition, some taxonomical notes are given at the end of the text, numerals of which are denoted by superscript in the list.

Authors' names combined with those of the species are abbreviated as follows: BALLION–BLN.; BATES–BTS.; BEHEIM–BHM.; BELOUSOV–BLS.; BREUNING–BR.; BŘEZINA–BRZ.; CAVAZZUTI–CV.; CHAUDOIR–CHD.; CRISTOFORIS–CRS.; DEJEAN–DJ.; DEUVE–DV.; DEYROLLE–DYZ.; FABRICIUS–FBR.; FAIRMAIRE–FRM.; FALDERMANN–

FLD.; FISCHER VON WALDHEIM—FS.; GANGLBAUER—GGL.; GÉHIN—GÉH.; GOTTWALD—GTW.; HAUSER—HSR.; HEINERTZ—HRZ.; HEINZ—HZ.; IMURA—IM.; ISHIKAWA—ISH.; KABAK—KB.; KALÁB—KLB.; KAMIYOSHI—KMY.; KLEINFELD—KL.; KORELL—KRL.; KRAATZ—KRT.; KRYZHANOVSKIY—KRY.; LAPOUGE—LP.; LASSALLE—LSL.; LEDOUX—LDX.; LINNÉ—L.; MANDL—MDL.; MANNERHEIM—MNH.; MÉNÉTRIÉS—MÉN.; MIZOGUCHI—MZG.; MIZUSAWA—MZS.; MORAWITZ—MRW.; MORVAN—MRV.; MOTSCHULSKY—MTS.; NAKANE—NKN.; OBYDOV—OBD.; PUTZEYS—PTZ.; REITTER—RT.; ROESCHKE—RSCH.; SEMENOV—SM.; SEMENOV-TIAN-SHANSKIY—SM.-T.-S.; SHILENKOV—SHL.; THOMSON—TMS.; ZAMOTAJLOV—ZMT.; ZNOJKO—ZNJ.; ZOLOTAREV—ZLT.

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Classification

Subtribe Carabina (all divisions *sedis mutabilis*)

1. Division Limnocarabigenici¹⁾

Genus *Limnocarabus* GÉHIN, 1876

Subgenus *Limnocarabus* GÉHIN, 1876

clathratus L., *maacki* MRW.

Subgenus *Euleptocarabus* NAKANE, 1956

porrecticollis BRS.

2. Division Chaetocarabigenici²⁾

Genus *Heterocarabus* MORAWITZ, 1886

marietti CRS. et JAN

Genus *Chaetocarabus* THOMSON, 1875

intricatus L. [*arcadicus* GISTL]

Genus *Platycarabus* MORAWITZ, 1886

(=*Pseudocechenus* MORAWITZ, 1886; *Baudiccarabus* GANGLBAUER, 1909)

depressus BONELLI, *irregularis* FBR. [*creutzeri* FBR., *cychroides* BAUDI, *fabricii* PANZER]

3. Division Hemicarabigenici³⁾

Genus *Hemicarabus* GÉHIN, 1885

macleayi DJ., *nitens* L., *serratus* SAY, *tuberculosis* DJ. et BOISDUVAL

Genus *Homoeocarabus* REITTER, 1896

maeander FS.

4. Division Ischnocarabigenici⁴⁾

Genus *Archicarabus* SEIDLITZ, 1887

(=*Aptocarabus* REITTER, 1896; *Deuteroicarabus* REITTER, 1896; *Nemoralus* SCHULER, 1976)

gotschi CHD., *monticola* DJ., *nemoralis* MÜLLER, *victor* FS. [*montivagus* PALLIARDI,

phoenix LP., *pseudomonticola* LP., *rossii* DJ., *steuartii* DYR., *wiedemanni* MÉN.]

Genus *Ischnocarabus* KRAATZ, 1877

[*cychropalpus* PEYRON, *tenuitarsis* KRT.]

Genus *Gnathocarabus* DEUVE, 1991

kusnetzovi SM.

5. Division Rhipocarabigenici⁵⁾

Genus *Rhipocarabus* REITTER, 1896

[*alysidotus* ILLIGER]

6. Division Apotomopterigenici⁶⁾

Genus *Apotomopterus* HOPE, 1838

[*angulihabitus* KL., *anxiensis* KL., *benardi* BR., *boulbenianus* DV., *bousquetellus* DV., *cheni* DV., *circe* CV. et RATTI, *datianshanicus* KL., *elliptipennis* DV., *fallettianus* DV., *feae* GESTRO, *fushuangensis* DV., *gigantothoracis* KL., *gracilithorax* DV., *guangdongicus* DV., *guangxicus* DV., *guzhangensis* KL., *helenae* KL., *hiekeianus* DV., *hubeicus* DV., *kasandra* KL., *lamarcki* DV., *lemoultianus* BR., *ludivinae* DV., *maoershanicus* CV., *menelaus* BR., *microtatos* CV., *ngi* DV., *odysseus* BR., *pervarius* KL., *pseudosemelai* CV., *saga* CV., *sino-elongatus* DV., *sinomeridionalis* DV., *thilliezi* DV., *thoracicus* CV., *trigintaduo* CV. et RATTI, *yuanbaoensis* DV., *yuanshanensis* KL., *yuellus* DV., *yunlingensis* DV., *yunnanicola* DV.]

Subgenus *Apotomopterus* HOPE, 1838

(=*Laocarabus* LAPOUGE, 1916; *Entomopterus* LAPOUGE, 1927)

arrowi HSR., *clermontianus* BR., *cyanopterus* HSR., *infirmior* HSR., *iris* IM., *laoshanicus* IM., *maolanensis* IM. et ZHOU [*adolescens* HSR., *aeneocupreus* HSR., *ajax* BR., *birmanus* ANDREWES, *breuningianus* LE MOULT, *cantonensis* HSR., *casaleianus* DV., *davidioides* DV. et YU, *davidis* DYR. et FRM., *eccoptopterus* KRT., *grossefoveatus* HSR., *inagakii* DV., *keithi* DV., *kryzhanovskianus* DV., *longeantennatus* HSR., *longicornis* FRM., *luschanensis* HSR., *mecynodes* BTS., *melli* BORN, *penelope* KL., *prattianus* BTS., *prodigus* ERICHSON, *shun* DV., *songshanicus* KL., *succyanipennis* IM., *telemachus* HSR., *vitalisi* LP., *yaophilus* DV., *yuae* DV., *yunanensis* BORN]

Subgenus *Dolichocarabus* LAPOUGE, 1927

(=*Siamocarabus* IMURA, 1989)

delavayi FRM., *tonkinensis* DV., *toulgoeti* DV., *tuxeni* MDL. [*koiwayai* DV. et IM., *kouan-*

ping MAINDRON, *madefactus* CV., *malaisei* BR., *masumotoi* IM., *solidior* DV. et IM., *tenuimanus* DV. et IM., *vogtae* BHM. et BR.]

Subgenus *Taiwanocarabus* IMURA et M. SATÔ, 1989⁷⁾

hupeensis HSR., *kouichii* IM. et MZS., *protenes* BTS., *sauteri* RSCH. [*ascendens* SM., *guizhouensis* CV., *ichangensis* BTS., ***masuzoi*** IM. et M. SATÔ, *novemunus* DV., *pseudotorquatus* DV., *skyaphilus* CV., *szetschuanus* BR., *tientei* TMS., *torquatus* CV., *wumingensis* DV., *xiaoxiangensis* DV.]

7. Division Lipastrigenici⁸⁾

1) Subdivision A (group of *Cyclocarabus*)

Genus *Cyclocarabus* REITTER, 1896

karaterekensis KLB., *martynovi* SM.-T.-S. et ZNJ., *minusculus* SM., ***namanganensis*** HEYDEN, *pseudolamprostus* KLB. [*aulacocnemus* SM., *belousovi* KB., *brosciformis* SM., *mniszehi* CHD., *pskemicus* DV. et KLB., *pullus* SM.-T.-S. et ZNJ., *zarudnyi* SM.-T.-S. et ZNJ.]

Genus *Ophiocarabus* REITTER, 1896⁹⁾

(=*Cryptocarabus* REITTER, 1896; *Haplocarabus* SEMENOV, 1898; *Microcarabus* ISHIKAWA, 1979)

aeneolus MRW., *angustatus* BLN., *kadyrbekovi* KB., *latiballioni* DV., *lindemanni* BLN., *rufus* BR., *sacorum* KB., ***striatus*** BLN. [*iliensis* KB., *imperfectus* SM., *iterates* BR., *kalabellus* DV., *kasantsevi* KB., *kirghisorum* KRY., *munganasti* RT., *parvicatenatus* MDL., *politulus* MRW., *praecox* SM., *regeli* MRW., *sororius* MRW., *subparallelus* BLN., *successor* RT., *tsharynensis* KB., *turkestanus* BR., *variabilis* BLN.]

2) Subdivision B (group of *Lipaster*)

Genus *Lipaster* MOTSCHULSKY, 1865

(=*Lamprocarabus* THOMSON, 1875; *Titanocechenus* BR. et RUSPOLI, 1970)

stjernvalli MNH.

Genus *Mimocarabus* GÉHIN, 1885

elbursensis BR., ***maurus*** ADAMS [*khorsanensis* DV., *pumilio* KÜSTER, *roseni* RT.]

Genus *Lyperocarabus* LAPOUGE, 1930

estreicheri FS., *mandibularis* FS., *sibiricus* FS. [*besseri* FS., *perrini* DJ., *planarius* OBD.]

Genus *Trachycarabus* GÉHIN, 1885

scabriusculus OLIVIER

Genus *Morphocarabus* GÉHIN, 1885

(=*Sajanocarabus* LUTSHNIK, 1924; *Amorphocarabus* LAPOUGE, 1930; *Basilicocarabus* LAPOUGE, 1930)

henningi FS., ***monilis*** FBR., *regalis* FS., *rothi* DJ., *scheidleri* PANZER [*excellens* FBR., *kozhantschikovi* LUTSHNIK, *mestscherjakovi* LUTSHNIK, *verzhtutskii* O. BERLOV et SHL., *zherichini* SHL.]

Genus *Apostocarabus* REITTER, 1896

chaudoiri GEBLER, ***odoratus*** Mts. [*karpinskii* KRY. et MATVEEV]

Genus *Pancarabus* REITTER, 1896

aeruginosiformis BR., ***aeruginosus*** FS., *eschsoltzi* MNH., *michailovi* KB., *spasskianus* FS.

Genus *Ancylocarabus* REITTER, 1896¹⁰⁾

- (=*Promorphocarabus* REITTER, 1896; *Gigantocarabus* SEMENOV, 1898)
gebleri FS., ***tarbagataicus* KRT.**
- Genus *Leptinocarabus* REITTER, 1896
 (= *Rhigoidocarabus* DEUVE, 1997)
hummeli FS., *latreillei* FS., ***venustus* MRW.**, *wulffi* MRW., *zhubajie* IM. [*coriaceipennis* CHD., *onjinsanicus* RAPUZZI]
8. Division Tachypigenici¹¹⁾
 Genus *Tachypus* WEBER, 1801
 (= *Autocarabus* SEIDLITZ, 1887)
***auratus* L.**
 Genus *Cancellocarabus* LUTSHNIK, 1924
***cancellatus* ILLIGER** [*vagans* OLIVIER]
9. Division Mesocarabigenici
 Genus *Mesocarabus* THOMSON, 1875
 (= *Hadrocarabus* THOMSON, 1875)
***problematicus* HERBST** [*dufourii* DJ., *lusitanicus* FBR.]
 Genus *Eupachycechenus* SEMENOV, 1898¹²⁾
***riffensis* FRM.**
10. Division Oreocarabigenici
 Genus *Oreocarabus* GÉHIN, 1876¹³⁾
***errans* GORY**, *ghiliani* LA FERTÉ-SÉNECTERE, *guadarramus* LA FERTÉ-SÉNECTERE]
11. Division Orinocarabigenici¹⁴⁾
 Genus *Orinocarabus* KRAATZ, 1878
concolor FBR., *fairmairei* TMS., *heteromorphus* DANIEL, *maritimus* SCHAUM, ***sylvestris* PANZER** [*adamellicola* GGL., *alpestris* STURM, *bertolinii* KRT., *carinthiacus* STURM, *castanopteris* A. & J. B. VILLA, *cenisius* KRT.]
12. Division Cavazzutiocarabigenici¹⁵⁾
 Genus *Cavazzutiocarabus* IMURA, 1998
***latreillei* DJ.**
13. Division Tmesicarabigenici¹⁶⁾
 Genus *Tmesicarabus* REITTER, 1896
***crisoforii* SPENCE**
14. Division Eurycarabigenici¹⁷⁾
 Genus *Eurycarabus* GÉHIN, 1885
 (= *Apatocarabus* SEMENOV, 1898)
***famini* DJ.** [*genei* GENÉ]
15. Division Nesaocarabigenici¹⁸⁾
 Genus *Nesaocarabus* BEDEL, 1895
 (= *Liocarabus* REITTER, 1896)
***interruptus* DJ.** [*coarctatus* BRULLÉ, *faustus* BRULLÉ]
16. Division Cytilocarabigenici
 Genus *Cytilocarabus* REITTER, 1896
***cribratus* QUENSEL**, *gemellatus* MÉN.

17. Division Pentacarabigenici
Genus *Pentacarabus* ISHIKAWA, 1972
harmandi L.P.
18. Division Pachycarabigenici
Genus *Pachycarabus* GÉHIN, 1876
(= *Caucasocarabus* LAPOUGE, 1930)
koenigi GGL., *roseri* FLD., *staehlini* ADAMS [imitator Rt., swaneticus Rt.]
19. Division Pachystigenici
Genus *Pachystus* MOTSCHULSKY, 1865
Subgenus *Euporocarabus* REITTER, 1896
hortensis L.
Subgenus *Pachystus* MOTSCHULSKY, 1865
(= *Melancarabus* THOMSON, 1875; *Phricocarabus* REITTER, 1896)
cavernosus FRIVALDSKY, *glabratus* PAYKULL, *tamsi* MÉN. [*graecus* DJ., *hungaricus* FBR., *pisidicus* PEYRON]
20. Division Meganebriigenici¹⁹⁾
Genus *Meganebrius* KRAATZ, 1895
(= *Parameganebrius* MANDL, 1970; *Makalubius* MANDL, 1985)
scheibei EIDAM, *swatensis* HRZ. [*alanstivelli* MRV., *arunensis* HRZ., *deliae* MRV., *dilatotarsalis* MDL., *epsteini* HRZ., *everesti* ANDREWES, *franzi* MDL., *granulatocostatus* MDL., *indicus* FRM., *kadoudali* MRV., *koganae* COLAS, *lebrethae* COLAS, *pseudoharmandi* MDL., *queinneci* DV., *salpansis* DV., *tamang* DV., *tuberculipennis* MDL., *wallichi* HOPE]
21. Division Piocarabigenici
Genus *Titanocarabus* BREUNING, 1933
sui IM. et ZHOU, *titanus* BR.
Genus *Piocarabus* REITTER, 1896
Subgenus *Piocarabus* REITTER, 1896
vladimirskiy DI. et BOISDUVAL
Subgenus *Qinlingocarabus* IMURA, 1998
(= *Heptacarabus* IMURA, 1998)
blumenthaliellus DV., *choui* DV.²⁰⁾, *kitawakianus* IM., *nanwutai* KL., KRL. et WRASE, *ohshimaianus* DV., *reitterianus* BR. [*laojunensis* KL.?²¹⁾]
22. Division Leptocarabigenici²²⁾
Genus *Aulonocarabus* REITTER, 1896
Subgenus *Weolseocarabus* KWON et LEE, 1984
koreanus RT.
Subgenus *Adelocarabus* REITTER, 1896
seishinensis LP., *seniopacus* RT. [*vogtianus* BHM. et BR.]
Subgenus *Aulonocarabus* REITTER, 1896
canaliculatus ADAMS, *kurilensis* LP. [*careniger* CHD., *gossarei* HAURY, *nangnimicus* BLUMENTHAL et DV., *pseudokoreanus* BR., *pukwonensis* DV. et MOURZINE]
Subgenus *Baptaulonocarabus* IMURA, 2002
truncaticollis ESCHSOLTZ [*gaskhewitschi* MTS., *kabakovi* LAFER, *kolymensis* LAFER,

mouthiezanus DV.]

Genus *Leptocarabus* GÉHIN, 1885

arboreus LEWIS, *hiurai* KMY. et MZG., *kumagaii* KIMURA et KOMIYA, *kyushuensis* NKN.,
procerulus CHD.

23. Division Rhigocarabigenici²³⁾

Genus *Zhongdianocarabus* IMURA, 2002

handelmazzettii MDL.

Genus *Batangocarabus* IMURA, 2002

itzingeri BR. [*batangicus* DV., *kozaburoi* IM.]

Genus *Araeocarabus* REITTER, 1896

roborowskii SM., *ladygini* SM.

Genus *Litangocarabus* IMURA, 2002

indigestus SM. [*subindigestus* DV., *turnai* DV.?, *xiangchengicus* DV.?]

Genus *Deqenocarabus* IMURA, 2002

rhododendron DV. et IM.

Genus *Zheduocarabus* IMURA, 2002

zheduoshanensis CV. [*jiulongensis* DV.]

Genus *Sinoleptocarabus* IMURA, 2002²⁴⁾

marcilhaci DV., *yokoe* DV.

Genus *Tibetorinocarabus* IMURA, 2002

laotse BR.

Genus *Syzygocarabus* SEMENOV, 1898

cateniger MRW. [*gracilicollis* SM.?]

Genus *Mianningocarabus* IMURA, 2002

confucius BR.

Genus *Rhigocarabus* REITTER, 1896

[*dacatraianus* DV., *morawitzianus* SM.]

Genus *Tachycarabus* SEMENOV, 1898

buddaicus SM., *gigolo* Hz. et Brz., *pseudopusio* DV., *pusio* SM. [*korsakowi* SM.?, *poeta* SM.?, *thais* Hz.?, *xiei* DV.?]

Genus *Sangocarabus* IMURA, 2002

maleki DV.

Genus *Hypsocarabus* SEMENOV, 1898

latro SM., *mikhaili* DV. et MOURZINE, *qinlingensis* IM. [*tewoensis* DV.]

24. Division Tomocarabigenici²⁵⁾

Genus *Rhytidocarabus* IMURA, 2002

scabripennis CHD. [*rumelicus* CHD., *simardianus* DV.]

Genus *Glossocarabus* IMURA, 2002

decolor FS.

Genus *Coreocarabus* IMURA, 2002

fraterculus RT.

Genus *Tomocarabus* REITTER, 1896

- (=*Procrustides* SEMENOV, 1905)
convexus FBR. [*bessarabicus* FS.]
 Genus *Asthenocarabus* LAPOUGE, 1930
opaculus PTZ.
 Genus *Callistocarabus* REITTER, 1896
marginalis FBR.
 Genus *Scambocarabus* REITTER, 1896
 (= *Eremocarabus* LAPOUGE, 1930)
kruberi FS. [*chaos* IM., *kruberoides* BR., *modestulus* SM., *sculptipennis* CHD., *shaanxiensis* DV.²⁶⁾]
 Genus *Stephanocarabus* IMURA, 1995²⁷⁾
 [*fraterculoides* BR.]
 Genus *Tanaocarabus* REITTER, 1896
sylvosus SAY
 Genus *Diocarabus* REITTER, 1896²⁸⁾
 (= *Allocarabus* LAPOUGE, 1921)
loschnikovi FS. [*aurocinctus* MTS., *beybienkoi* KRY., *caustomarginatus* IM. et MZS., *dorogostaiskii* SHL., *massagetus* MTS.]
 Genus *Watanabeocarabus* IMURA, 2002
slovtzovi MNH.
 Genus *Cryocarabus* LAPOUGE, 1930²⁹⁾
 [*chamissonis* FS.]
 Genus *Neocarabus* LAPOUGE, 1931
taedatus FBR.
 Genus *Durangocarabus* IMURA, 2002
forreri BTS. [*hendrichsi* BOLÍVAR y PIELTAIN, ROTGER et CORONADO]
 Genus *Zoocarabus* REITTER, 1896
bogdanowi BLN. [*cicatricosulus* MRW.]
 Genus *Ulocarabus* REITTER, 1896
 (= *Bactrocarabus* SEMENOV, 1927)
stschurovskii SOLSKY [*theanus* RT.]
 Genus *Coccocarabus* IMURA, 2002
minimus SM.-T.-S. et ZNJ.
 Genus *Carpathophilus* REITTER, 1896
linnei PANZER
 Genus *Semnocarabus* REITTER, 1896
 (= *Anthracarabus* LAPOUGE, 1930)
carbonicolor MRW., *erosus* MTS., *regulus* DOHRN, *transiliensis* SM. [*mullerellus* BHM. et BR.]
25. Division Carabigenici³⁰⁾
 Genus *Carabus* LINNÉ, 1758
 (= *Eutelocarabus* REITTER, 1896; *Apocarabus* LAPOUGE, 1930; *Nippocarabus* LAPOUGE,

1930)

arcensis HERBST, *deyrollei* GORY, ***granulatus* L.**, *sculpturatus* MÉN., *vanvolxemi* PTZ.
[*menetriesi* HUMMEL, *stscheglowi* MNH.]

Genus *Eucarabus* GÉHIN, 1885

Subgenus *Eucarabus* GÉHIN, 1885

(=*Loxocarabus* REITTER, 1896; *Xystrocarabus* REITTER, 1896)

catenulatus SCOPOLI, *italicus* DJ. [*obsoletus* STURM, *parreyssi* PALLIARDI, ***ulrichi* GER-**
MAR]

Subgenus *Tylocarabus* REITTER, 1896

***cumanus* Fs.**

Subgenus *Parhomopterus* LAPOUGE, 1931

(=*Orientocarabus* KWON et LEE, 1984)

billbergi MNH., *cartereti* DV., *manifestus* KRT., *namhaedoensis* KWON et LEE, *nitididor-*
sus ISH. et KIM, ***sternbergi* RSCH.** [*angustus* RSCH., *mianyangensis* DV. et LI, *olliveiri-*
anus DV., *pawlowskianus* DV., *szeli* DV., *xiuyanensis* DV. et LI]

Genus *Lichnocarabus* REITTER, 1896

limbatus SAY [***vinctus* WEBER**]

Genus *Archaeocarabus* SEMENOV, 1898

(=*Acoptopterus* LAPOUGE, 1927)

dongchuanicus DV., *koidei* IM., *latipennis* BR., *morphocaraboides* DV., *nanosomus* HSR.,
nestor BR., *paris* BR., *pseudolatipennis* DV., *striatus* SM. [*agamemnon* BR., *anhuinus*
IM., *battoniensis* DV., *bornianus* HSR., *camilloi* CV. et RATTI, *claricollis* CV. et RATTI,
daiyunshan KL., *dreuxioides* DV., *emanuelei* IM., *fontellus* DV., *fuscomarginatus* KL.,
kucerae DV., *kweitshauensis* MDL., *latens* CV. et RATTI, *oblongior* DV., ***relictus* SM.**,
shamaevi IM., *tianbaoshan* KL., *tieguanzi* IM., *vigilax* BTS., *wuangxianus* KL., *wushan-*
ling KL., *xingshanensis* IM., *xupuensis* KL., *yunnanus* FRM.]

Genus *Acrocarabus* LAPOUGE, 1931

callisthenoides SM., ***guerini* Fs.**

Genus *Isiocarabus* REITTER, 1896

***fiduciaris* TMS.**, *miaorum* LSL. et PRUNIER [*castanopterus* HSR., *dargei* DV., *dayongen-*
sis KL., *dreuxi* DV., *gressittianus* MDL., *hienfoungi* TMS., *kiukiangensis* BTS., *pustululatus*
DV.]

Genus *Ohomopterus* REITTER, 1896³¹⁾

albrechti MRW., *arrowianus* BR., *daisen* NKN., ***dehaanii* CHD.**, *esakii* CSIKI, *insulicola*
CHD., *iawakianus* NKN., *japonicus* MTS., *kawanoi* KMY. et MZG., *kimurai* ISH.,
lewisianus BR., *maiyanus* BTS., *tosanus* NKN., IGA et UENO, *uenoi* ISH., *yaconinus*
BTS., *yamato* NKN.

26. Division Ctenocarabigenici³²⁾

Genus *Ctenocarabus* THOMSON, 1875

***galicianus* GORY**

Genus *Rhabdotocarabus* SEIDLITZ, 1887

***melancholicus* FBR.**

27. Division Hygrocarabigenici³³⁾

Genus *Hygrocarabus* THOMSON, 1875

- nodulosus* CREUTZER [*variolosus* FBR.]
 28. Division Cathopliigenici³⁴⁾
 Genus *Cathoplius* THOMSON, 1875
 (= *Cychocephalus* GÉHIN, 1875)
asperatus DI.
 29. Division Procrustigenici³⁵⁾
 1) Subdivision A (group of *Macrothorax*)³⁶⁾
 Genus *Chrysocarabus* THOMSON, 1875
 Subgenus *Chrysocarabus* THOMSON, 1875
auronitens FBR. [*lineatus* DI., *splendens* OLIVIER]
 Subgenus *Chrysotribax* REITTER, 1896
hispanus FBR., *rutilans* DI.
 Genus *Iniopachys* SOLIER, 1848³⁷⁾
 [*auriculatus* PTZ., *pyrenaicus* AUDINET-SERVILLE]
 Genus *Macrothorax* DESMAREST, 1850
 (= *Dichocarabus* REITTER, 1896; *Dorcarabus* REITTER, 1896; *Paracarabus* REITTER, 1896)
morbillosus FBR. [*planatus* CHD., *rugosus* FBR.]
 Genus *Sellaecarabus* STURANI, 1947³⁸⁾
 (= *Dysmictocarabus* PUISSÉGUR, 1964)
olympiae SELLA [*solieri* DI.]
 Genus *Sphodristocarabus* GÉHIN, 1885
 (= *Sphodristus* THOMSON, 1875)
adamsi ADAMS, *bohenanni* MËN., *heinzi* BR., *macrogonus* CHD., *scovitzi* FLD., *varians* FS. [*coruhnehriensis* CV., *elegantulus* MTS., *enigmaticus* HZ., *esperanzae* HZ., *georgia* CV., *giachinoi* CV., *gilnickii* DYR., *kindermanni* CHD., *korgei* HZ., *kurdicus* HZ., *pavesii* CV., *rotundicollis* MDL., *tokatenis* RSCH.]
 Genus *Relictocarabus* LEDOUX, 1984³⁹⁾
meurguesae LDX.]
 Genus *Apolestus* DEUVE, 1990⁴⁰⁾
 [*deuvei* LSL., *legrandi* DV., *omphreodes* Rt., *pseudodepressus* MACHARD]
 Genus *Imaibius* BATES, 1889⁴¹⁾
 (= *Tropidocarabus* KRAATZ, 1895; *Parimaibius* BREUNING, 1958; *Lithariophorus* MANDL, 1985)
baronii HRZ., *pachtoun* LDX. [*anami* LDX., *barysomus* BTS., *boysi* TATUM, *cashmirensis* REDTENBACHER, *cavifrons* MDL., *dardiellus* BTS., *epipreuralis* SM., *erberi* HZ., *gandharae* HRZ., *gridellii* BR., *isabellae* LSL., *kabakovianus* GTW., *kaghanensis* HRZ., *leepai* HZ., *nouristani* LDX., *piiffi* MDL., *rositanus* SM., *stoliczkanus* BTS.]
 2) Subdivision B (group of *Tribax*)⁴²⁾
 Genus *Tribax* FISCHER, 1817⁴³⁾
 (= *Platychrus* KOLENATI, 1845; *Neoplectes* REITTER, 1885; *Archiplectes* GOTTWALD, 1982; *Microtribax* GOTTWALD, 1982)
agnatus GGL., *circassicus* GGL., *kasbekianus* KRT., *osseticus* ADAMS, *puschkini* ADAMS, *reitteri* RETOWSKI, *starcki* HEYDEN, *starekianus* GGL., *titan* ZLT. [*adelphus* ROST, *apollo*

ZLT., *apschuanus* ROST, *balkaricus* BLS. et ABDURACHMANOV, *biebersteini* MÉN., *certus* RT., *compressus* CHD., *curllettii* CV., *daphnis* KURNAKOV, *edithae* RT., *edmundi* SM., *ibericus* FS., *jason* SM., *kasakorum* SM., *koltzei* ROST, *komarowi* RT., *kraatzii* CHD., *kratkyi* GGL., *lailensis* BLS., *lederi* RT., *macropus* CHD., *mellyi* CHD., *merdeniki* CV. et KRL., *nothus* ADAMS, *plasoni* GGL., *polychrous* ROST, *prometheus* RT., *protensus* SCHAUM, *satyrus* KURNAKOV, *shtchurovi* BLS. et ZMT., *steveni* MÉN.]

Genus *Microplectes* REITTER, 1896

cupreus CHD. [*riedeli* MÉN.]

Genus *Cechenochilus* MOTSCHULSKY, 1850⁴⁴⁾

Subgenus *Cechenochilus* MOTSCHULSKY, 1850

boeberi ADAMS [*lazorum* BLS. et ZMT.]

Subgenus *Procechenochilus* IMURA et BELOUSOV, 2002

heydenianus STARCK [*adagensis* GTW., *gusevi* ZMT., *kokujewi* SM.]

3) Subdivision C (group of *Procrustes*)⁴⁵⁾

Genus *Pachycranion* SOLIER, 1848

Subgenus *Aulacocarabus* GÉHIN, 1876

exaratus QUENSEL, *carinatus* MTS. [*dejeani* FS., *planicollis* KÜSTER]

Subgenus *Proteocarabus* GÉHIN, 1876

violaceus L.

Subgenus *Pachycranion* SOLIER, 1848

(=*Carabulus* LUTSHNIK, 1924; *Ainocarabus* MANDL., 1973; *Nabicarabus* KWON et LEE, 1984)

amoenus CHD., *imperialis* FS., *kolbei* RSCH., *leachi* FS., *schoenherri* FS., *vietinghoffi* ADAMS [*avinovi* SM.-T.-S. et ZNJ., *danilevskii* OBD., *obovatus* FS.]

Genus *Protomegodontus* IMURA, 2002⁴⁶⁾

germarii STURM

Genus *Procerus* DEJEAN, 1828

Subgenus *Procerus* DEJEAN, 1828

gigas CREUTZER, *scabrosus* OLIVIER [*syriacus* KOLLAR]

Subgenus *Megodontus* SOLIER, 1848⁴⁷⁾

bonvouloiri CHD., *stroganowi* ZOUBKOFF, *persianus* RSCH. [*caelatus* FBR., *croaticus* DJ.]

Genus *Procrustes* BONELLI, 1809⁴⁸⁾

Subgenus *Procrustes* BONELLI, 1809

(=*Procrusticus* WHITE, 1845; *Macrogenus* MOTSCHULSKY, 1846; *Sphodristus* MOTSCHULSKY, 1865; *Pseudoprocrustes* MORAWITZ, 1886)

chevrolati CRS. et JAN, *coriaceus* L., *punctatus* CASTELNAU [*anatolicus* CHD., *banoni* DJ., *clypeatus* ADAMS, *payafa* WHITE]

Subgenus *Creprostus* IMURA, nov.⁴⁹⁾

talyschensis MÉN.

Subgenus *Lamprostus* MOTSCHULSKY, 1865

(=*Chaetogaster* LAPOUGE, 1930)

calleyi FS., *erenleriensis* HZ. et KORGE, *nordmanni* CHD., *prasinus* MÉN., *torosus* FRIVALDSKY [*lecordieri* DV., *renardi* CHD., *sauleyi* PIOCHARD]

- Subgenus *Oxycarabus* SEMENOV, 1898
saphyrinus CRS. et JAN
- Subgenus *Chaetomelas* THOMSON, 1875
 (= *Procrustocarabus* GÉHIN, 1876; *Chaetoprostus* REITTER, 1896)
asperatus MULSANT, *ehrenbergi* KLUG, *hemprichi* DI., *impressus* KLUG, *syrus* RSCH.
- 4) Subdivision D (group of *Cratocephalus*)⁵⁰⁾
 Genus *Cratophyrtus* REITTER, 1896⁵¹⁾
kaufmanni SOLSKY [hauseri RT., medvedevi KRY., nikolajevi KB., turcosinensis MDL.]
 Genus *Pseudotribax* KRAATZ, 1884⁵²⁾
ferghanicus BR., *validus* KRT.]
- Genus *Pantophyrtus* THIEME, 1881
brachypedilus MRW., *turcomannorum* THIEME [debilis SM., longipedatus BLS. et KB., punctatostriatus HEYDEN]
- Genus *Goniocarabus* GÉHIN, 1885⁵³⁾
 (= *Alagocarabus* MORAWITZ, 1886; *Acarabus* SEMENOV, 1890)
caerulans MRW., *gracilis* KRAATZ, *grombcewskii* SM., *gussakovskii* KRY., *perelloi* CASALE, *stackelbergi* KRY., *tadzhikistanus* KRY.]
- Genus *Cratocarabus* REITTER, 1896
jacobsoni SM. [gorodinskii OBD., kryzhanovskii BOGACHEV, *puer* MRW., *redikortzewi* SM. et BR.]
- Genus *Cratocechenus* REITTER, 1896
akinini MRW. [ovtchinnikovi GTW., znojkoï SM. et BR.]
- Genus *Cratocephalus* KIRSCH, 1857
cicatricosus FS., *corrugis* DOHRN [chan BR.]
- Genus *Eotribax* SEMENOV, 1898
eous MRW., *hiekei* KB. et KRY.⁵⁴⁾, *valikhanovi* KB. [eokirgisicus KB., foreli HSR., karkarensis KB. et OVCHINNIKOV, malkovskiy KB., manap BRZ. et KB., rufescens BR., semenovianus BR.]
- Genus *Deroplectes* REITTER, 1895
 (= *Plesius* SEMENOV, 1905)
staudingeri GGL. [concinus SM., dokhtourovski GGL., klapperichianus MDL., *sphinx* RT.]
- Genus *Axinocarabus* MORAWITZ, 1886⁵⁵⁾
 [fedtschenkoi SOLSKY]
- Genus *Cechenotribax* SEMENOV-TIAN-SHANSKIJ et ZNOJKO, 1932
petri SM.-T.-S. et ZNJ.
- Genus *Pachycechenus* SEMENOV, 1898⁵⁶⁾
balassogloi DOHRN, *solskii* BLN. [nicolasi LP.]
- Genus *Alipaster* REITTER, 1896
pupulus MRW. [barovskii SM.-T.-S. et ZNJ., infantulus MRW., rueckbeili BR., shirtalensis GTW., thianshanskii BR.]
- Genus *Leptoplesius* REITTER, 1898
merzbacheri HSR. [dolini DV., dolonicus OBD., kleinfeldorum KB. et PUTCHKOV, latiusculus DV., *marquardtii* RT., shokalskii SM. et BR., subtilistriatus HSR.]

5) Subdivision E (group of *Damaster*)⁵⁷⁾Genus *Pseudocoptolabrus* REITTER, 1896⁵⁸⁾(=*Protodamaster* IMURA et KEZUKA, 1989; *Nigracoptolabrus* DEUVE, 1991)
burmanensis BR., *nosei* IM., ***taliensis* FRM.** [*armiger* IM., *branaungi* IM.]Genus *Megodontoides* DEUVE, 1991***erwini* MDL.** [*poschingerianus* KRL. et KL., *promachus* BTS., *thibetanus* BR.]Genus *Acathaicus* REITTER, 1896⁵⁹⁾(=*Cathaicodes* REITTER, 1896)***alexandrae* SM.**Genus *Coptolabrodes* BŘEZINA et IMURA, 1997⁶⁰⁾***haeckeli* BŘZ. et IM.**Genus *Imaibiodes* DEUVE, 1991***businskyi* DV.**Genus *Lasiocoptolabrus* IMURA, 1993***sunwukong* IM.**Genus *Aristocarabus* SEMENOV, 1896***viridifossulatus* FRM.**Genus *Pagocarabus* MORAWITZ, 1886Subgenus *Shunichiocarabus* IMURA, 1995⁶¹⁾***uenoianus* IM.**Subgenus *Pagocarabus* MORAWITZ, 1886⁶²⁾***crassesculptus* KRT.** [*crassethoracis* KL.]Genus *Sigenacarabus* KLEINFELD, 2000⁶³⁾***sigena* KL.**Genus *Eccoptolabrus* SEMENOV, 1898⁶⁴⁾***exiguus* SM.**Genus *Calocarabus* SEMENOV, 1887(=*Calocechenus* REITTER, 1896; *Cryptocechenus* SEMENOV, 1898)*aristochroides* DV. [***gratus* SM.**, *guinanensis* DV., *janatai* BŘZ., *juengerianus* KL., *kalabi* DV., *linxiaensis* DV., *przewalskii* MRW., *sifanicus* SM., *trichothorax* BŘZ. et IM., *turnai* DV.]Genus *Neoplesius* REITTER, 1896⁶⁵⁾(=*Indocarabus* LAPOUGE, 1930; *Eocechenus* SEMENOV-TIAN-SHANSKIJ et ZNOJKO, 1932; *Cupreocarabus* DEUVE, 1997)*alpherakii* SM., *hengduanicola* DV., *kaschkarowi* SM., *lama* SM., *leptoplesioides* DV., *lixianensis* DV., *ludmilae* DV., *markamensis* DV., *nanschanicus* SM., *sichuanicola* DV., ***wagae* FRM.** [*borodini* HZ., *brezinai* DV., *bruggeianus* DV., *danae* KLB., *ditomoides* DV., *draco* BŘZ., *folwarcznyi* DV., *glasunowi* HZ., *glinkai* HZ., *huangi* DV., *hummelioides* DV., *kamensis* DV., *kaznakovi* SM.-T.-S. et ZNJ., *kocmani* KLB., *kozloviellus* SM.-T.-S. et ZNJ., *laevithorax* BR., *micromentum* DV. et IM., *morettoii* DV., *morvanellus* DV., *mouthiezinoides* DV. et KLB., *noctivagus* DV., *panda* DV., *paulusi* KLB., *pseudohuangi* DV., *pseudomarkamensis* DV., *saueri* DV., *sinotibeticola* MDL., *takashimai* DV. et IM., *tatsienlui* BR., *trachynodes* BTS., *tsogoensis* DV., *yanjinganus* IM. et MZS., *yushuensis* DV.]

Genus *Pseudocranion* REITTER, 1896(=*Cratocranion* SEMENOV, 1898)

benjamini SM., ***gansuensis*** SM., *remondianus* DV., *sackeni* SM., *wenxianicola* DV., *zhanglaensis* DV. [*alliciens* DV., *fumigatus* SM., *gonggaicus* DV., *jiudingensis* DV., *kitawakiellus* IM., *labrangicus* DV., *lazikouensis* DV., *meditabundus* DV., *pseudoremondianus* DV., *pseudosackeni* DV., *sackenioides* DV., *shuamaluko* DV., *sinicus* BR., *taibai-shanicus* DV., *tibetanophilus* DV., *viatorum* DV.]

Genus *Damaster* KOLLAR, 1836(=*Adamaster* REITTER, 1896)***blaptoides*** KOLLAR⁶⁶⁾Genus *Cephalornis* SEMENOV, 1889(=*Cychrocarabus* MORAWITZ, 1889)***potanini*** SM.Genus *Cychrostomus* REITTER, 1896⁶⁷⁾[***anchocephalus*** RT., *pseudoprosodes* SM.-T.-S. et ZNJ.]Genus *Teratocarabus* SEMENOV-TIAN-SHANSKIJ et ZNOJKO, 1932⁶⁸⁾[***azrael*** SM.-T.-S. et ZNJ.]Genus *Fulgenticarabus* DEUVE et LI, 1998⁶⁹⁾[***flutschi*** DV. et LI]Genus *Acoptolabrus* MORAWITZ, 1886⁷⁰⁾Subgenus *Yezacoptolabrus* IMURA, 2002***gehinii*** FRM., *lopatini* MRW.Subgenus *Acoptolabrus* MORAWITZ, 1886(=*Koreacoptolabrus* KWON et LEE, 1984)

constricticollis KRT., *leechi* BTS., *mirabilissimus* ISH. et DV., ***schrencki*** MTS. [*changeon-leei* ISH. et KIM]

Genus *Eupachys* CHAUDOIR, 1857⁷¹⁾***glyptopterus*** FS. [*acutithorax* DV.]Genus *Shenocoptolabrus* IMURA, ZHOU et SU, 1999***osawai*** IM., ZHOU et SUGenus *Cathaicus* BATES, 1870⁷²⁾***brandti*** FLD.Genus *Coptolabrus* SOLIER, 1848⁷³⁾

(=*Coptolabrinus* REITTER, 1897; *Eocarabus* SEMENOV, 1898; *Eucoptolabrus* SEMENOV, 1898; *Nesocoptolabrus* LAPOUGE, 1930)

augustus BTS., *formosus* SM., *fruhstorferi* RSCH., *ignimitellus* BTS., *jankowskii* OBERTHÜR, *kubani* DV., *lafossei* FEISTHAMEL, *nankotaizanus* KANO, *principalis* BTS., *pustulifer* LUCAS, ***smaragdinus*** FS. [*elysii* TMS., *gemmifer* FRM., *ishizukai* DV. et OHSHIMA]

Notes

¹⁾ For detailed molecular phylogeny of the Limnocarabigenici, see IMURA, KIM *et al.* (1998).

²⁾ For detailed molecular phylogeny of the Chaetocarabigenici, see IMURA, SU & OSAWA

(2000 b). Another molecular data given by CASALE *et al.* (1998) also reveal that *Platycarabus* is a well-defined monophyletic group, though the number of the base-pairs analyzed in their study is too small to draw a persuasive conclusion.

³⁾ For detailed molecular phylogeny of the Hemicarabigenici, see SU, IMURA *et al.* (2000).

⁴⁾ For detailed molecular phylogeny of the Ischnocarabigenici, see IMURA, SU & OSAWA (2000 a). Systematic position of *Ischnocarabus* is still tentative, since we have no molecular data on both of two species belonging to this taxon. In view of the morphology and the zoogeography, however, it is most plausible that *Ischnocarabus* is clustered together with the *Archicarabus*–*Gnathocarabus* complex, so that this division is named Ischnocarabigenici as determined here.

⁵⁾ Since nothing has been known on the DNA sequences of *alysidotus*, it is difficult at present to determine the correct systematic position of this taxon within the subtribe Carabina. However, I tentatively regard this unique carabid as forming a distinct division composed of a single monotypical genus *Rhipocarabus*, because of the highest modification of its male genital organ, i.e., a large membranous preostium, unusually developed ostium lobe and strongly deformed endophallus, etc.

⁶⁾ For detailed molecular phylogeny of the Apotomopterigenici, see IMURA, KIM *et al.* (1998) and KIM, SU *et al.* (1999). Although involving a large number of species, *Apotomopterus* is considered to be a well-defined monophyletic genus, and may be split into three major subgenera as shown here (for the subgeneric classification, see OSAWA, SU & IMURA, 2002, p. 76; that suggested by IMURA, KIM *et al.*, 1998, p. 22, contains a misjudgment on this matter). For the assignment of the DNA-unknown species, I have regarded the endophallic features as most diagnostic. As to the remaining species whose endophallic structure is still unknown, I have avoided to give a subgeneric classification and listed them up only as belonging to the genus *Apotomopterus*.

⁷⁾ I adopt *Taiwanocarabus* as the representative name of this subgenus, since the endophallus of its type species, *masuzoi*, agrees in basic structure with that of *sauteri*. In my view, these two species seem to have been derived from a common ancestor in the Island of Taiwan. If *masuzoi* falls into a different lineage on the molecular genealogical tree, proposal of a new subgeneric name will be necessary.

⁸⁾ For detailed molecular phylogeny of the Lipastrigenici, see OSAWA, SU & IMURA (2002, pp. 76–81).

⁹⁾ So far as the analyzed species are concerned, *Ophiocarabus* and *Cryptocarabus* are hardly distinguishable from each other on the molecular tree, though they have been currently distinguished into two different groups. These two higher taxa are therefore unified into a single genus, adopting *Ophiocarabus* as the representative name.

¹⁰⁾ Of the two oldest available names (*Ancylocarabus* for *tarbagataicus* and *Promorphocarabus* for *gebleri*) described simultaneously by REITTER (1896), I adopt *Ancylocarabus*, since it was first revised as a distinct subgenus by LAPOUGE (1932, p. 648).

¹¹⁾ For detailed molecular phylogeny of the divisions from No. 8 (Tachypigenici) to 24 (Tomocarabigenici), see IMURA, SU *et al.*, (1998) and OSAWA, SU & IMURA (2002, pp. 81–98).

¹²⁾ *Eupachycechenus* was proposed by SEMENOV (1898) for a peculiar North African species, *riffensis*, though usually synonymized with *Mesocarabus* by current authors. In my view, however, it should be regarded as occupying an independent position in the Carabina, because of its uniquely shaped endophallus and isolated distributional area. Here I provisionally give this taxon the rank with generic importance and place it at the side of *Mesocarabus*.

¹³⁾ Since we have no molecular data on any species belonging to *Oreocarabus*, systematic position of this group is uncertain. However, it is highly plausible that this Iberian carabid is a close relative of either *Orinocarabus* or *Mesocarabus*, judging from the morphological and the zoogeographical viewpoints. In this paper, I tentatively regard *Oreocarabus* as forming a distinct division, and

place it between the Mesocarabigenici and the Orinocarabigenici.

¹⁴⁾ For detailed molecular phylogeny and endophallic morphology of the Orinocarabigenici, see IMURA, SU *et al.* (1998).

¹⁵⁾ For the details on this peculiar Alpine carabid, see IMURA (1998) and IMURA, SU *et al.* (1998).

¹⁶⁾ This small carabid beetle endemic to the Pyrenees has been placed in *Tachypus* (= *Auto-carabus*) by current taxonomists (*e.g.*, DEUVE, 1994; IMURA & MIZUSAWA, 1996; BŘEZINA, 1999). On the ND5 tree, however, it shows no direct relatedness to *Tachypus* but forms a highly independent branch, suggesting that its emergence may be traced back to the time of radiation of the Carabina (OSAWA, SU & IMURA, 2002, pp. 83, 86–87). It is therefore regarded as forming a distinct position with divisional importance.

¹⁷⁾ For the details of the Eurycarabigenici, see OSAWA, SU & IMURA (2002, pp. 83–87). According to the molecular data presented by PRÜSER, BRÜCKNER & MOSSAKOWSKI (2000), a unique Mediterranean species, *genei*, surely belongs to this division. As to the relationships between *Eurycarabus* and *Nesaeocarabus*, see the following paragraph.

¹⁸⁾ For the details of Nesaeocarabigenici, see OSAWA, SU & IMURA (2002, pp. 83–87). Another molecular data given by PRÜSER, BRÜCKNER & MOSSAKOWSKI (2000) strongly suggest that *Nesaeocarabus* is a sister taxon of *Eurycarabus*. On more reliable ND5 trees shown by OSAWA *et al.*, which cover nearly all the important higher taxa from the world, however, these two taxa only show a remote affinity supported by lower bootstrap confidence level and the branching point is very deep. It is plausible that these two taxa were derived from a common ancestor long ago, but I regard each of them as corresponding to two respective divisions. According to PRÜSER *et al.*, a species endemic to the Gran Canaria Island, *coarctatus*, surely belongs to the genus *Nesaeocarabus*.

¹⁹⁾ It is uncertain whether the division Meganebriigenici is strictly uniform or not, since our knowledge is still too poor on the molecular phylogeny of this series. Judging from considerably variable endophallic features and rather isolated distributional area of each species, it may be better to classify the division into several distinct genera.

²⁰⁾ For the details on the true systematic position of *choui*, see OSAWA, SU & IMURA (2002, pp. 84, 89, 206–207).

²¹⁾ This least known species was described by KLEINFELD (1999) as a member of *Rhigocarabus*. However, the occurrence of *Rhigocarabus* in Henan Province can be disputed, since this series seems confined to the Tibetan plateau, extending the eastern periphery of its distributional range at most to northern Sichuan and southern Gansu. KLEINFELD's species should correctly be classified into the *Qinlingocarabus* lineage as shown here, though we have to wait for further examination of the DNA sequences and at least the endophallic structure to clarify its true affinity.

²²⁾ For detailed molecular phylogeny of the Leptocarabigenici, see KIM, TOMINAGA *et al.* (2000), KIM, ZHOU *et al.* (2000) and OSAWA, SU & IMURA (2002, pp. 89–96, 177–183).

²³⁾ For detailed findings on the morphology and the molecular phylogeny of the Rhigocarabigenici, see OSAWA, SU & IMURA (2002, pp. 83–84) and IMURA (2002). Concerning the species denoted with question mark, the molecular data or at least the detailed morphological findings of the endophallus are indispensable to clarify their true systematic positions.

²⁴⁾ For the taxonomical assignment of *Sinoleptocarabus*, see IMURA (2002). For further particulars, see KIM, ZHOU *et al.* (2000), SU, IMURA & OSAWA, (2001) and OSAWA, SU & IMURA (2002, pp. 89–96, 210–213).

²⁵⁾ For the details on the molecular phylogeny of the Tomocarabigenici and its component genera recently described, see OSAWA, SU & IMURA (2002, p. 86) and IMURA (2002).

²⁶⁾ Although placed tentatively in the genus *Scambocarabus*, *shaanxiensis* is assumed to be a member of another independent genus, as has been suggested by the molecular genealogical tree

(OSAWA, SU & IMURA, 2002, p. 86).

²⁷⁾ The DNA sequences of *Stephanocarabus* are not yet analyzed. Here I tentatively place this unique Gansu carabid at the side of *Scambocarabus*, mainly due to a close resemblance in the male genitalic features.

²⁸⁾ As has been elucidated by the molecular study, the heterogeneity of the so-called *Diocarabus* series is apparent (OSAWA, SU & IMURA, 2002, pp. 81–98; see also IMURA, 2002, for the descriptions of several new genera). Although I tentatively placed all the DNA-unknown species in the genus *Diocarabus*, some of them may have to be transferred to another or new lineage according to the coming molecular data.

²⁹⁾ The DNA sequences of *chamissonis* are still unknown. Judging from peculiarly shaped endophallus, e.g., strongly deformed and pigmented praeputial pad, I give an independent position with generic importance to this unique Alaskan species.

³⁰⁾ For detailed molecular phylogeny of the Carabigenici, see OSAWA, SU & IMURA (2002, pp. 98–104). Note that *Acrocarabus* is not a constituent of the Ischnocarabigenici but apparently belongs to this division (IMURA, SU & OSAWA, 2000 a; OSAWA, SU & IMURA, 2002, pp. 74, 101, 234).

³¹⁾ Viewed from the molecular phylogeny, specific and infraspecific classifications of the genus *Ohomopterus* remain indisposed (cf. SU, TOMINAGA *et al.*, 1996; TOMINAGA, SU *et al.*, 2000; OSAWA, SU & IMURA, 2002, pp. 154–176, etc.). Here I conventionally adopt sixteen species in accordance with the morphological classification currently made on the basis of male genitalic features.

³²⁾ Systematic position of *Ctenocarabus* has been variable according to the authors (e.g., a section in the subgenus *Tribax* (!) of the Carabi Longimandibulares *sensu* BREUNING, 1932; a subgenus in the Procrustimorphi of the Multistriati *sensu* IMURA, 1996; ditto in the Longimandibulares of the Lobifera *sensu* DEUVE, 1997). On the molecular genealogical tree, however, it is derived from near the root of the large cluster of the Carabina (OSAWA, SU & IMURA, 2002, pp.105–106), and should be regarded as a distinct division. *Rhabdotocarabus* (often synonymized with *Ctenocarabus*) apparently shows an affinity with *Ctenocarabus* on the tree, but the branching point between these two taxa is very deep. *Rhabdotocarabus* is also much different in the basic structure of the endophallus from *Ctenocarabus*. They are therefore separated into two distinct genera, though unified into a single division.

³³⁾ For the systematic position of the Hygrocarabigenici assigned from the molecular data, see IMURA, SU & OSAWA (2000 b) and OSAWA, SU & IMURA (2002, p. 73, fig. 5-11).

³⁴⁾ Systematic position of a unique North African carabid, *Cathoplius*, has been variable according to the authors, since it has a series of peculiar morphological features (e.g., a subgenus in the Multistriati *sensu* BREUNING, 1932; ditto in the Procrustimorphi of the Multistriati *sensu* IMURA, 1996; ditto in the Longimandibulares of the Lobifera *sensu* DEUVE, 1997). On the ND5 tree, this taxon seems to be highly isolated without showing any phylogenetic affinity to the other groups. It is therefore regarded as a distinct division in the subtribe Carabina (OSAWA, SU & IMURA, 2002, pp. 104–106).

³⁵⁾ For detailed molecular phylogeny of the Procrustigenici, see OSAWA, SU & IMURA (2002, pp. 104–124). This is the largest and most strikingly differentiated group of the Carabina, though well defined as a single division on the genealogical tree. The Procrustigenici is radiated at first to five large phyletic series almost corresponding to the distributional zone, as classified in the present system into the subdivisions A to E. For further particulars, see the lines of each subdivision described below.

³⁶⁾ For detailed molecular phylogeny of the subdivision A (group of *Macrothorax*, or the European group *sensu* OSAWA, SU & IMURA, 2002), see OSAWA, SU & IMURA (2002, pp. 109–110).

³⁷⁾ Systematic position of *Iniopachys* has been variable according to the authors, mainly due to

overestimation of the macrocephalism. For example, BREUNING (1932) placed it in the subgenus *Cechenus* together with several other large-headed taxa occurring in Caucasia, Central Asia and China. Viewed from the basic structure of endophallus and the distributional area, however, it is most plausible that *Iniopachys* belongs to the subdivision A (group of *Macrothorax*) of the Procrustigenici, and should be placed at the side of *Chrysocarabus*, though we must not jump at a conclusion until its DNA sequences will be analyzed.

³⁸⁾ Although often regarded as one of the members of *Chrysocarabus*, a unique Alpine species *olympiae* forms a highly independent branch on the tree, and should be discriminated as a full genus within the subdivision A. I also placed another elegant species, *solieri*, in the same genus, since basic structure of the male genitalic organ of *solieri* well agrees with that of *olympiae*. This view is supported by the result drawn from another molecular work by DÜRING *et al.* (2001).

³⁹⁾ Systematic position of *Relictocarabus* is not definitive until its molecular data will be introduced into science, though there is little doubt regarding this higher taxon as belonging to the division Procrustigenici. In the present list, I place it in the group of *Macrothorax*, mainly due to characteristic features of the endophallus and the distributional area (strictly confined to a part of the Grand Atlas Mountains in Morocco).

⁴⁰⁾ This unique and least known carabid is known so far only from the arid plateau in eastern Turkey. Though we have no molecular data on any species belonging to this series, I provisionally place it at the side of *Relictocarabus*, mainly due to similarity in the endophallic structure.

⁴¹⁾ The *Imaibius* complex is unified into a single genus in the present list, but this arrangement is excessively tentative. There remain too many races whose DNA sequences are unknown as yet, and so-called *Imaibius* might be discriminated into several distinct lineages at the subgeneric level or even generic.

⁴²⁾ For detailed molecular phylogeny of the subdivision B (group of *Tribax*, or the Caucasian group *sensu* OSAWA, SU & IMURA, 2002), see OSAWA, SU & IMURA (2002, pp. 110–112).

⁴³⁾ *Archiplectes* was established by GOTTWALD (1982) as a distinct subgenus to discriminate a number of species with peculiar features from *Tribax* (s. str.), and this arrangement has been adopted by many authors but DEUVE (1991, '94), who synonymized GOTTWALD's taxon with *Tribax*. In view of the molecular phylogeny, the species morphologically belonging to *Tribax* and those belonging to *Archiplectes* are intermingled in the same cluster without forming the subgenus-specific clade, suggesting that the morphology does not run parallel with the molecular phylogeny, so far as the analyzed species are concerned. Here I tentatively unified all the species into a single genus *Tribax*, though subgeneric classification within the genus must be revised after analyzing much more samples. Also I synonymized both *Microtribax* and *Neoplectes* with the same genus, though their DNA sequences are still unknown.

⁴⁴⁾ For the details of the molecular phylogeny and the morphology of the genus *Cechenochilus*, see OSAWA, SU & IMURA (2002, p. 110–112) and IMURA & BELOUSOV (2002).

⁴⁵⁾ For detailed molecular phylogeny of the subdivision C (group of *Procrustes*, or the Pan-Eurasian group *sensu* OSAWA, SU & IMURA, 2002), see OSAWA, SU & IMURA (2002, pp. 112–118).

⁴⁶⁾ For the details of the genus *Protomegodontus*, see IMURA (2002).

⁴⁷⁾ Although I apply *Megodontus* to this subgenus, this arrangement is still tentative, since we have not yet analyzed the DNA sequences of *caelatus*, the type species of *Megodontus*.

⁴⁸⁾ For detailed molecular phylogeny of the genus *Procrustes*, see OSAWA, SU & IMURA (2002, pp. 112–118). On the ND5 tree, *Procrustes* forms a large cluster which is further split into five major subclusters corresponding respectively to five distinct subgenera, though the result of molecular phylogeny does not necessarily run parallel with what has been drawn from the morphology. Note that *Oxycarabus* belongs to this lineage beyond all doubt.

⁴⁹⁾ *Creprostus* IMURA, subgen. nov. (type species: *Carabus talyschensis* MÉNÉTRIÉS, 1832). On the molecular genealogical tree (OSAWA, SU & IMURA, 2002, pp. 105–106, 113–114), *Procrustes talyschensis* is clearly discriminated from other members of the same genus by forming an independent cluster. It is therefore worth distinguishing as a new subgenus. *Description*:— A large-sized carabid beetle belonging to the genus *Procrustes* of the division Procrustigenici (in the present sense). Most closely allied to *Procrustes* (s. str.), particularly in the external features, but differs from that subgenus by the following respects: 1) median part of labrum much more conspicuously protruded anteriorly and remarkably convex above; 2) elytral sculpture reduced to form multiple rows of small granules; 3) male genitalia with the ostium lobe very long, narrow and not bilobed at tip, basal lateral lobes absent, median lobe not strongly inflated, prepraeputial lobes hemispherically inflated and almost symmetrical, scales covering the inflexed side not strongly pigmented. The new subgeneric name is an anagram of *Procrustes*.

⁵⁰⁾ For detailed molecular phylogeny of the subdivision D (group of *Cratocephalus*, or the Tianshanese group *sensu* OSAWA, SU & IMURA, 2002), see OSAWA, SU & IMURA (2002, pp. 117–118). In this subdivision, there are many discrepancies between the morphological classification and the molecular phylogeny, above all in such genera as *Cratophyrtus*, *Pantophyrtus* and *Leptoplesius*, as well as a part of *Eotribax*, *Cratocarabus* and *Cratocechenus*. Their phylogeny and taxonomy must be revised after analyzing sufficient number of samples.

⁵¹⁾ On the molecular genealogical tree, the species morphologically identified with “*Cratophyrtus kaufmanni*” appears divided into two different lineages, suggesting that the morphologically defined *Cratophyrtus* complex is not strictly uniform.

⁵²⁾ Nothing has been known on the DNA sequences of the species belonging to *Pseudotribax*. I tentatively regard this higher taxon as a distinct genus, and place it at the side of *Cratophyrtus*.

⁵³⁾ Also nothing has been known on the DNA sequences of the species belonging to *Goniocarabus*, and its systematic position remains unsolved. Judging from the endophallic structure, however, *Goniocarabus* may have a certain affinity with *Pantophyrtus*, though markedly different in the shape of the head, above all of the mouth part. It is probable that they have been derived from a common ancestor and evolved into two different lineages according to the feeding habit; one with cyclohrized mouth part and the other with hypertrophic head.

⁵⁴⁾ Although I tentatively placed *hiekei* in the genus *Eotribax* in accordance with currently used classification, this species is clustered together with “*Cratocarabus*” *jacobsoni* and “*Cratocechenus*” *akinini elisabethae* on the ND5 tree. The classification of these taxa should be revised at both the specific and generic levels after analyzing much more samples.

⁵⁵⁾ Though we have no molecular data on *Axinocarabus*, I tentatively place this genus at the side of *Deroplectes* on the basis of the morphological findings. Both the genera bear several common characters in detailed structure of the endophallus (e.g., presence of a paraligula).

⁵⁶⁾ Two macrocephalic species, *solskyi* and *balassogloi*, have been regarded by most authors as nothing but the true components of *Cratocephalus*. However, both the species belong to an independent clade without showing any relatedness with *Cratocephalus* in a strict sense. They are therefore regarded as forming a distinct genus, applying *Pachycechenus* as the representative name.

⁵⁷⁾ For detailed molecular phylogeny of the subdivision E (group of *Damaster*, or the Chinese group *sensu* OSAWA, SU & IMURA, 2002), see OSAWA, SU & IMURA (2002, pp. 118–124).

⁵⁸⁾ Viewed from the molecular phylogeny, *Pseudocoptolabrus* is one of the oldest elements of the subdivision E (group of *Damaster*) diverged at the very beginning of its radiation. Although morphologically classified into several distinct species, each showing a remarkable geographical variation, phylogenetic distances among each species/subspecies belonging to this genus seem to be very small, so far as the analyzed taxa are concerned.

⁵⁹⁾ *Acatahaicus* occupies an independent position in the large cluster corresponding to the subdivision E, showing no direct relatedness with two other macrocephalic genera, *Eupachys* and *Cathaicus*.

⁶⁰⁾ In their check list recently published, KLEINFELD & SCHÜTZE (1999) synonymized *Coptolabrodes* with superficially resembling *Acoptolabrus* on an unsounded basis. This inference is, however, utterly wrong; the phylogenetic independence of *Coptolabrodes* is supported from both the morphology and molecular phylogeny, as shown in the original description (BŘEZINA & IMURA, 1997) and in the genealogical trees presented by OSAWA, SU & IMURA (2002, pp. 105–106, fig. 5-31, pp. 119, fig. 5-37, pp. 203, 9-2).

⁶¹⁾ There is little doubt that *Shunichiocarabus* is the closest relative of *Pagocarabus*, since both the taxa are clustered together with rather shallow branching point supported by 100% of the bootstrap confidence level (OSAWA, SU & IMURA, 2002, pp. 105–106, 119). A close affinity of these two taxa is proved also from the morphology, since they share several common characters such as hypertrophic anterior tooth of the right mandibular retinaculum, basically well-agreeing genitalic features, etc. It is probable that *Shunichiocarabus* (endemic to the Dabashans and the Dashennongjia) is a replaced component of *Pagocarabus* which is rather widely distributed in North-Central China.

⁶²⁾ *Pagocarabus* has been used in a very wide sense by several authors, putting nearly all the species belonging to *Neoplesius* in it. However, these two higher taxa should be discriminated from each other, as has been elucidated by the molecular genealogical tree. The subgenus *Pagocarabus* should be restricted to the type species, *crassesculptus*, and its direct relatives.

⁶³⁾ According to Zhi-Hui SU (pers. comm.) who already analyzed the DNA sequences of *Sigenacarabus*, this unique carabid beetle forms an independent branch in the cluster of the subdivision E, and should be regarded as a distinct genus.

⁶⁴⁾ In spite of much different external features, the closest relative of *Eccoptolabrus* is assumed to be *Calocarabus*, as shown by the molecular genealogical tree (OSAWA, SU & IMURA, 2002, pp. 105–106, 119).

⁶⁵⁾ Phylogenetic relationships among the species belonging to such higher taxa as *Neoplesius*, *Eoecchenus*, *Cupreocarabus* and *Pseudocranion* is complicated, since they seem to be intermingled on the molecular phylogenetic tree (OSAWA, SU & IMURA, 2002, p. 119, fig. 5-37). It is obvious that the morphology does not necessarily run parallel with the phylogeny in this complex (cf. IMURA, ZHOU *et al.*, 1998). Here I divide them roughly into two large genera, *Neoplesius* and *Pseudocranion*, yet this opinion is exceedingly conventional.

⁶⁶⁾ For detailed molecular phylogeny of the genus *Damaster*, see SU, OHAMA *et al.* (1996), SU, TOMINAGA *et al.* (1998) and OSAWA, SU & IMURA (2002, pp. 186–198). Though the type species, *blaptoides*, has been regarded as a single polytypical species by most taxonomists, it is clearly divided into eight distinct lineages differentiated long ago on the ND5 tree.

⁶⁷⁾ We have no analytical data on the DNA sequences of *Cychrostomus*. In many respects, however, this taxon is nothing but a member of the subdivision E, and I provisionally place it at the side of *Cephalornis*. Another candidate for the relative of *Cychrostomus* is assumed to be the *Acoptolabrus* (s. str.) – *Eupachys* complex.

⁶⁸⁾ Although nothing has been known on the DNA sequences of *Teratocarabus*, it is most plausible that this least known taxon belongs to the subdivision E, and is not so far from the *Acoptolabrus* (s. str.) – *Eupachys* complex.

⁶⁹⁾ Since I know this taxon only through the literature, its systematic position cannot be determined precisely. In the original description, DEUVE & LI (1998) compared it with *Megodontus* and *Cathaicus*. In my view, however, the closest relative of *Fulgenticarabus* is assumed to be *Teratocarabus*. To solve the problem, we have to wait for the molecular data, or at least the findings of the

male genital organ. Incidentally, there are two problems on the type locality of this taxon. According to the original description (the paper was written under a joint authorship of DEUVE and MOURZINE, but the descriptions of several taxa including those of *Fulgenticarabus* and its type species *flutschii* were made by DEUVE and LI), the type locality of *flutschii* is “Heilongjiang, Yichang, Hongxing, Linchang”. It is obvious that *Yichang* is the misspelling of Yichun [伊春], a city situated in the north-central part of the Heilongjiang Province, surely containing Hongxing [红星] in its territory. *Linchang* [林场] does not indicate the name of a certain place but only means the timberland in English. There is a large number of “linchang=timberland” around Hongxing, and it is almost impossible to specify the exact collecting site of this interesting species.

⁷⁰⁾ For detailed molecular phylogeny and subgeneric classification of the genus *Acoptolabrus*, see OKAMOTO (1999), OSAWA, SU & IMURA (2002, pp. 119–122, 149–150, 198–200) and IMURA (2002).

⁷¹⁾ This unique carabid beetle is characterized by black and mat body surface, remarkably enlarged head and strongly developed mandibles, and has been placed near *Cathaicus* and *Acatahaicus* by most authors. To our surprise, however, it is considered to be a sister taxon of *Acoptolabrus* (s. str.), since these two are clustered together on the molecular genealogical tree with 100% of bootstrap confidence level at the branching point (SU, IMURA & OSAWA, 2001; OSAWA, SU & IMURA, 2002, pp. 105–106, 119, 121). In view of the molecular phylogeny, *Eupachys* and *Acoptolabrus* (s. str.) seem to have been derived from a common ancestor beyond all doubt.

⁷²⁾ As mentioned in the preceding lines, *Cathaicus* has been regarded as belonging to the “*Acatahaicus*–*Eupachys*” complex. On the ND5 tree, however, it is no doubt involved in the cluster of *Coptolabrus*, suggesting the fact that *Cathaicus* is a sister taxon of *Coptolabrus* (SU, IMURA & OSAWA, 2001; OSAWA, SU & IMURA, 2002, pp. 105–106, 119, 121–122).

⁷³⁾ *Coptolabrus* forms a well-defined cluster on the molecular genealogical tree, and yet its classification at the species level is not as simple as deduced from the morphology. In particular, that between the two species, *smaragdinus* and *jankowskii*, seems to be very hard to deal with (OSAWA, SU & IMURA, 2002, p. 122, fig. 5-38).

要 約

井村有希：分子系統に基づくオサムシ亜族の上位分類。—— オサムシ亜族の上位分類体系は、幾多の変遷を経て今日に至っている。過去の体系は、成虫の外部形態、幼虫頭部の形態、あるいは雄交尾器内袋など、いずれも形態形質に基づいて構築されてきたが、研究者ごとに重視する形質が著しく異なっていたため、結果的に各著者の好み色が濃く反映された類型分類の域を出ることができず、いまだに国際的なコンセンサスを得たスタンダードな体系というものが存在しない。ここ数年、大澤省三をはじめとするわが国の研究グループによって精力的に進められたミトコンドリアDNAの分析に基づく分子系統解析は、すでに同亜族を構成する上位群（属、亜属）の9割以上、総種数の4割以上を網羅する材料の分析を終え、分子系統樹によって示された系統関係に基づいて上位分類を語ることが可能な域に達している。本論文では、主としてミトコンドリアDNAのND5遺伝子領域における1,069塩基対の分析に基づき、NJ法およびUPGMAにより構築された分子系統樹（すべて、大澤、蘇、井村をはじめとするオサムシの分子系統研究グループにより発表されたもの）を詳しく検討し、これまでの概念と異なるまったく新しいオサムシ亜族の上位分類の再構築を試みた。分類にあたっては、分子系統樹の結果をリンネ式階層に反映するためにいくつかの規定を設けた。すなわち、オサムシ亜族の一

斉放散により誕生した独立性の高いグループを群 (division) とみなし、群よりも下位のレベルで明らかに単系統とみなしうるまとまった集団を属とみなす。また、基本形態が明らかに異なるものは、分子系統的には同一属とみなしえても、便宜上、別属として区別する。分子系統樹の上で明らかに異なる系列に出現するものは、たとえ基本形態の差が僅少であっても別属として区別する。DNAが未分析のものに関しては、形態、分布、生態等の知見を考慮に入れて、暫定的ながらその分類学的位置を定める、等である。この規定のもとでは、世界のオサムシ亜族は29群、137属に分類される。

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